Reference: *Biol. Bull.*, **148**: 461–471. (June, 1975)

STUDIES ON THE REPRODUCTIVE SYSTEMS OF SEA-STARS. II. THE MORPHOLOGY AND HISTOLOGY OF THE GONODUCT OF *ASTERIAS VULGARIS*[1]

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Although they are directly involved in the important process of shedding gametes, the gonoducts of asteroids have been described in structural terms for only a few species. In fact, the question of whether gonoducts exist in some sea-stars was debated for many years (Müller and Troschel, 1842; Greeff, 1872; Hoffman, 1872; and Ludwig and Hamann, 1899). Those investigators who have studied the gonoducts of asteroids consider either the morphology or the histology of only limited regions of the duct. The general orientation of the gonoduct in the ray is outlined by Müller and Troschel (1842) for *Asterias rubens* and *Crossaster papposus*, by M. Sars (1861) for *Pteraster pulvillus* and *P. militaris*, by Cuénot (1887) for *Marthasterias glacialis*, and by Richters (1912) for *Linckia multiforis*. The histology of the gonoduct is described in a preliminary way by Ludwig (1878) for *Asterina pentagona*, by Hamann (1885) for *Asterias rubens*, and by Gemmill (1911, 1912, and 1914) for *Solaster endeca* and *Asterias rubens*. Some details of the nature of the epithelial cells of the gonoduct of *Asterina gibbosa* are revealed in the ultrastructural studies of Buslé (1969). The present work, dealing with *Asterias vulgaris*, gives a detailed description of the morphology and histology of the entire gonoduct; observations are made on the reproductive systems of immature and mature specimens of both sexes. Such information, provided by integrating morphological and histological observations, will serve as a basis for comparison with the gonoducts of other asteroids and is necessary in interpreting the activities of this important part of the reproductive system.

Materials and Methods

Procedures for sexually mature specimens

Twenty-five of the sea-stars used in this study are the same specimens obtained in "major collections" and studied in an earlier work concerning the morphology and histology of the wall of the gonad of *Asterias vulgaris;* methods of identifying, measuring, dissecting, fixing, embedding, and sectioning these specimens have already been described in some detail (Walker, 1974). Two interradii from each of these specimens were stained for use in studies of the morphology and histology of the gonoduct. One entire interradius was stained with Mallory's Phosphotungstic Acid Haematoxylin (PTAH) (Lillie, 1965) for observations on the general histology of the gonoduct. Wherever possible, the number of subsidiary gonoducts (see observations) in each unit of the reproductive

[1] This paper represents part of a thesis submitted to the Graduate School of Cornell University in partial fulfillment of the requirements for the degree of Master of Science.

system was recorded. The 2 gonoducts in another interradius were stained with aldehyde fuchsin (Cameron and Steele, 1959) to indicate the presence of elastic connective tissue in the gonoduct.

Collection of small sea-stars

In addition to the 25 sexually mature specimens from the "major collections," 54 small sea-stars, with R values (R is the length from the center of the disc along the aboral surface of the ray to the tip) ranging from 8 to 24 mm, were collected from a variety of locations on the windward side of Star Island, New Hampshire. Thirty were identified as *Asterias vulgaris* on the basis of their major pedicellariae, which were of the elongate pointed variety characteristic of this species. These specimens were fixed and decalcified in Bouin's fluid, dehydrated in ethanol, embedded in paraffin in a vacuum oven, and sectioned at 9 to 12 μ. All specimens were routinely stained with PTAH and were used to investigate the development of the gonoduct.

Wax model

To aid in visualizing the complicated structural details of Region A of the gonoduct (see observations), a three-dimensional wax model was constructed for a sexually mature specimen of each sex. The model was based on 40 serial longitudinal sections of the gonoduct that had all been stained with PTAH. A greatly enlarged wax section was cut to conform to the projected image of each histological section (Sack, 1966); the wax sections were then carefully assembled and studied.

Observations

The reproductive system of normal 5-rayed specimens of *Asterias vulgaris* consists of 10 separate units, each including a gonad, genital branches of the aboral haemal and coelomic (perihaemal) rings, and a gonoduct (Fig. 1). Two units are found in a ray, one attached to either side above the supramarginal ossicles. The gonad is a single large bag-like structure that is composed of two distinct groups of tissues, the outer and inner sacs; the genital branches of the aboral haemal and coelomic (perihaemal) rings which extend from the disc to the gonad are continuous with the haemal and genital coelomic (perihaemal) sinuses, respectively, that are important features in the structure of the wall of the gonad (Walker, 1974).

The gonoduct forms rather late in the life of the sea-star. In the specimens of *Asterias vulgaris* examined in this study, no trace of gonoducts was evident in specimens smaller than 14 mm ray-length. When the gonoduct is first apparent in animals ranging from 15–18 mm ray-length, it is represented by a knob of tissue at the upper or aboral end of the gonad (Fig. 2); even in animals of this size all 10 gonoducts do not begin to form at the same time. In this study, the gonoduct was first recognizable as a completed structure in animals with rays measuring 34 mm, where it is a tube with a single external opening. From its orifice within the gonad, the gonoduct passes through the stalk suspending the gonad and is

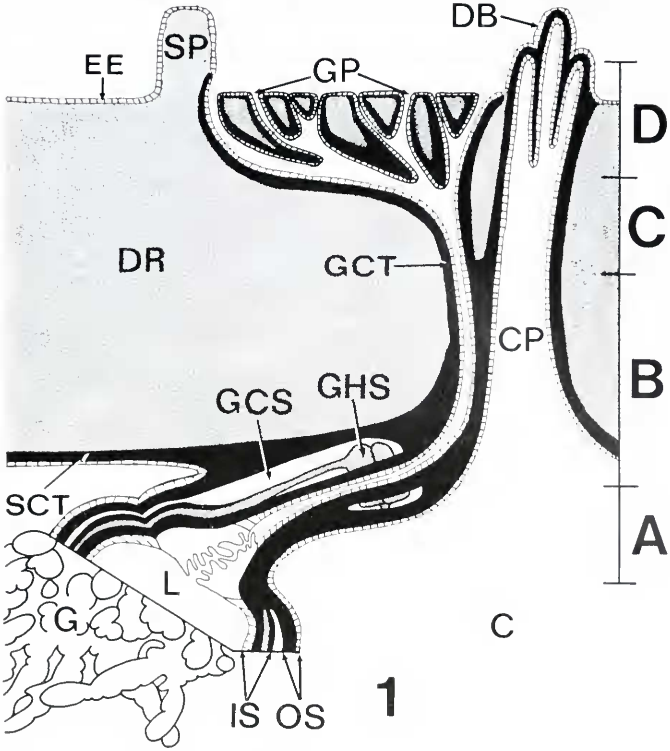

FIGURE 1. Diagrammatic representation of one unit of the reproductive system of *Asterias vulgaris,* showing its major components: the gonad, the gonoduct, and genital branches of the aboral haemal and coelomic (perihaemal) rings. The gonad is shown in external view, while the rest of the unit is shown in longitudinal section. The proportions of various parts of the unit are not representative of their actual dimensions, as several areas are magnified for clarity. Regions A, B, C, and D of the gonoduct are shown in the diagram. Symbols used are: C, coelom; CP; coelomic pocket; DB, dermal branchiae; DR, dermis; EE, external epithelium; G, gonad; GCS, genital coelomic (perihaemal) sinus; GCT, connective tissue of the gonoduct; GHS, genital haemal strand; GP, gonopores; IS, inner sac of the gonad; L, lumen of the gonad; OS, outer sac of the gonad; SCT, subperitoneal connective tissue; SP, spine on a dorsolateral ossicle.

thereafter intimately associated with various tissues in the wall of the ray. As it passes from the gonad to the body wall, the gonoduct accompanies genital branches of the aboral haemal and coelomic (perihaemal) rings, and it follows these proximally and aborally for a variable distance; in section this relationship appears as in Figure 3. The gonoduct soon loses its relationship with the genital branches of the aboral haemal and coelomic (perihaemal) rings and enters a pocket in the body wall that is continuous with the general perivisceral coelom (Figs. 1 and 4, CP); this coelomic pocket leads toward the surface of the ray and subdivides to form the lumina of several dermal branchiae (Fig. 1, DB). It is lined by typical parietal peritoneum underlain by a layer of collagenous connective issue, called the subperitoneal connective tissue layer (Walker, 1974); the gonoduct passes

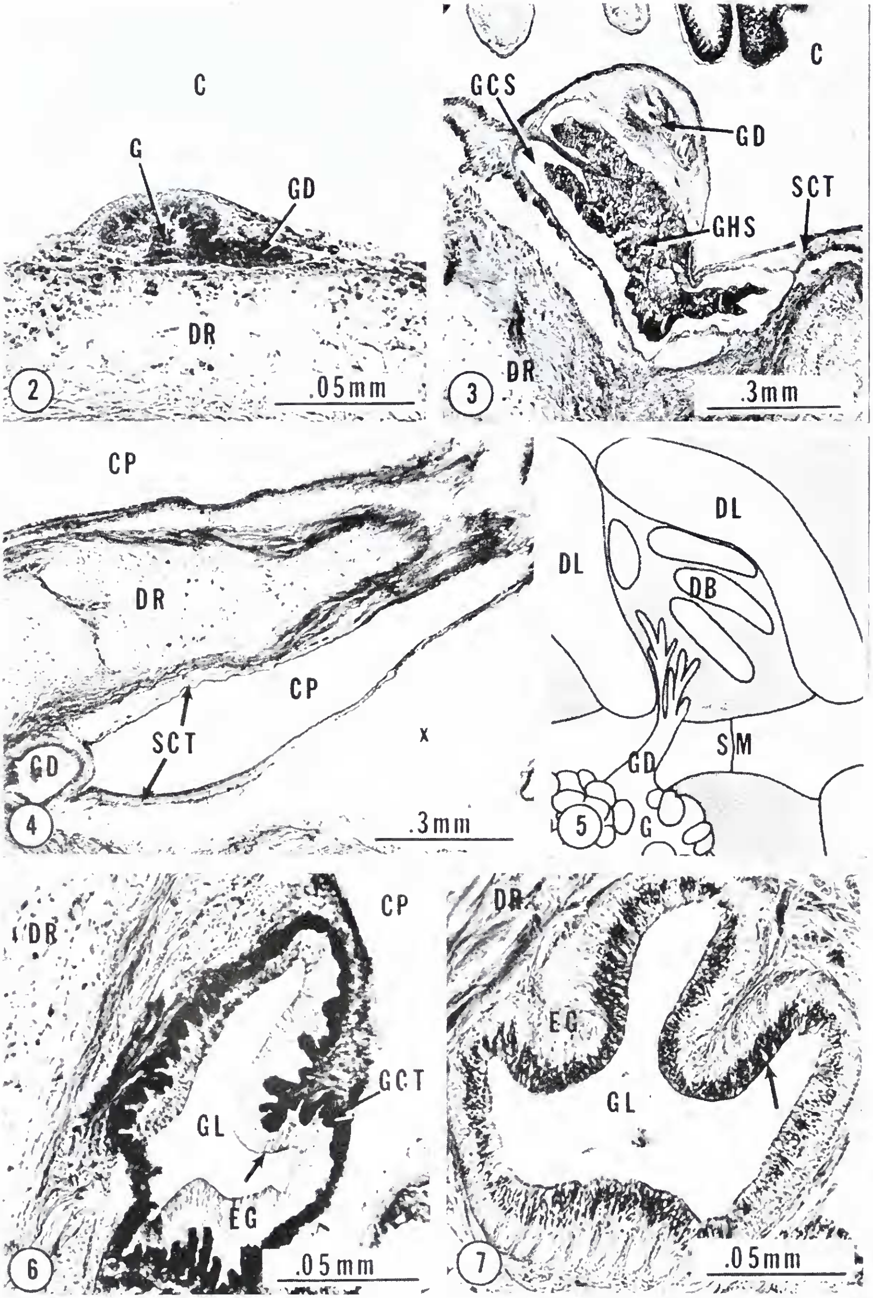

FIGURE 2. Section of the wall of the ray (R = 18 mm), showing a sexually immature gonad and the bud of the gonoduct (PTAH). Symbols used are: C, coelom; DR, dermis; G, gonad; GD, gonoduct.

FIGURE 3. Section of the wall of the ray near the point of attachment of the gonad, showing the relationships of the gonoduct and genital branches of the aboral haemal and

along one wall of the coelomic pocket within the subperitoneal connective tissue (Figs. 1 and 4, SCT). It is by means of this pocket that the gonoduct is brought near the surface of the ray without actually making its way independently through the entire dermis. In the region where dermal branchiae first branch from the coelomic pocket, the gonoduct leaves the subperitoneal connective tissue of the pocket, penetrates the dermis, and passes the remaining distance to the external epithelium. Within the dermis of young animals, the gonoduct forms a tube with a single lumen that is continuous to the outside; in older animals subsidiary gonoducts form from the primary duct and each passes separately to the surface of the ray. Subsidiary ducts may also be subdivided; one male specimen (R = 56 mm) examined in this study had 17 distinct subsidiary gonoducts associated with one gonad. The number of such ducts in one reproductive unit bears no relationship to that in any other unit in the same sea-star.

Unlike the conspicuous gonopores of *Marthasterias glacialis* (Cuénot, 1887) or those of *Leptasterias groenlandica* (Lieberkind, 1920), which are set on knobs of epithelium, the gonopores of *Asterias vulgaris* are flush with the surface of the ray and are extremely difficult to distinguish with the unaided eye. Only during or just after spawning are they readily observable. They open aborally on the interradial surface of the ray in an interossicular space which is penetrated by several dermal branchiae. The dermal branchiae open internally into a coelomic pocket which is located below the space. The interossicular space is one of hundreds present in the body wall and is bounded orally by supramarginal ossicles and aborally by two to many dorsolateral ossicles (Fig. 5). Gonopores found within the space bounded by these ossicles open in the external epithelium covering either the space or the dorsolateral ossicles themselves.

In terms of its histology, the gonoduct is an extension of the inner sac of the gonad (Fig. 1, IS) (Walker, 1974). The tubular duct is composed of an outer connective tissue layer that is continuous with the inner and outer walls of the haemal sinus of the gonad and also an inner epithelial layer which is continuous with the germinal epithelium of the gonad. No genital haemal strand lies within the connective tissue of the gonoduct and neither muscle nor nerve fibers are recognizable among the epithelial cells lining the gonoduct.

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coelomic (perihaemal) rings (PTAH). Symbols used are: C, coelom; DR, dermis; GCS, genital coelomic (perihaemal) sinus; GD, gonoduct; GHS, genital haemal strand; SCT, subperitoneal connective tissue layer.

FIGURE 4. A section of the wall of the ray, showing the relationship of the gonoduct and a coelomic pocket (PTAH). The × marks a large region formed as tissues have lost their normal connection to the dermis. Symbols used are: CP, coelomic pocket; DR, dermis; GD, gonoduct; SCT, subperitoneal connective tissue layer.

FIGURE 5. Diagrammatic representation of the inner lateral wall of the ray showing an interossicular space and also the relationship of the gonad and the gonoduct to the ossicles of the ray. Symbols used are: DB, dermal branchiae; DL, dorsolateral ossicles; G, gonad; GD, gonoduct; SM, supramarginal ossicles.

FIGURE 6. Cross-section of Region B of the gonoduct; notice the dark staining folded connective tissue layer (Aldehyde fuchsin). The arrow indicates a vacuolated cell. Symbols used are: CP, coelomic pocket; DR, dermis; EG, epithelium of the gonoduct; GCT, connective tissue of the gonoduct; GL, lumen of the gonoduct.

FIGURE 7. Cross-section of Region C of the gonoduct, showing the typical disposition of the epithelial and connective tissue layers (PTAH). The arrow indicates a vacuolated cell. Symbols used are: DR, dermis; EG, epithelium of the gonoduct; GL, lumen of the gonoduct.

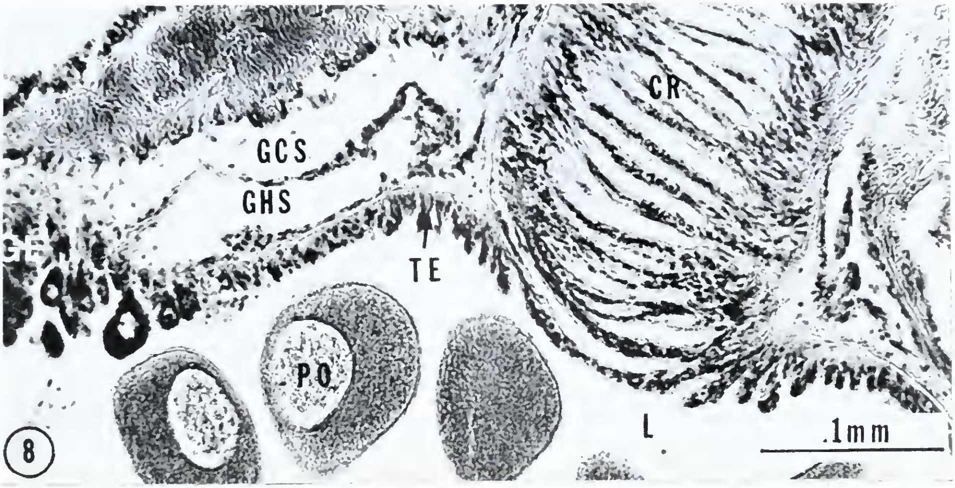
The outer connective tissue layer is characteristically thrown into ridges which run longitudinally along the length of the gonoduct; the fibers of this layer also run longitudinally along the axis of the duct, and they stain darkly with aldehyde fuchsin (Fig. 6). Toward the lumen of the gonoduct, these ridges of connective tissue support the epithelium of the gonoduct which is composed of common flagellated and scattered vacuolated cells (Figs. 6 and 7, EG and arrows). The flagellated cells form a pseudostratified epithelium of crowded columnar cells, often with extremely attenuated bases. Nuclei are usually ovoid with their long axes oriented perpendicularly to the basement membrane. At its free end, each cell bears a single flagellum that rises from a distinct basal body. In favorable preparations, a clear brush border of microvilli is evident. The vacuolated cells are found along the length of the gonoduct of either sex among the much more common flagellated cells. Typically, each contains a large ovoid vacuole, with maximum dimensions of $5\ \mu \times 12\ \mu$, which may be located at any height in the layer of cells. Often these vacuoles appear to open into the lumen of the gonoduct.

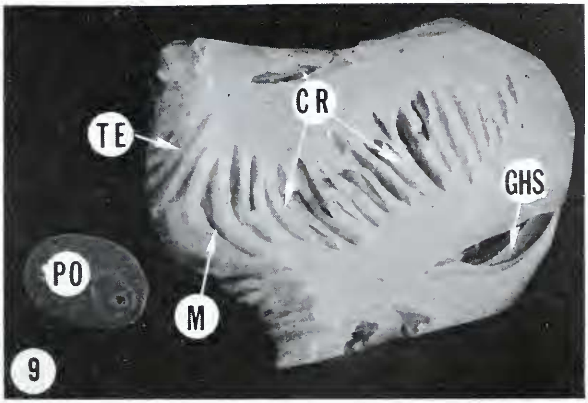
To facilitate further description, the gonoduct has arbitrarily been divided into four regions along its length (Fig. 1; A, B, C, and D).

Region A: although this is the shortest portion of the gonoduct it is at the same time the most complex in terms of the relationships of its connective tissue and in terms of the complexity of its epithelial layer. This is an area of transition between the tissues of the inner sac of the gonad and those of the gonoduct. It is in this region that the gonoduct first forms an association with the subperitoneal connective tissue layer. The stalk suspending the gonad is a cylinder of connective tissue which is continuous between the connective tissue of the outer sac of the gonad and the subperitoneal connective tissue of the body wall. As the gonoduct passes through this cylinder, its connective tissue fibers become firmly knitted on one side to those of the stalk; later, in Region B, the gonoduct is completely surrounded by the subperitoneal connective tissue layer (Fig. 1).

The epithelium lining the lumen of the gonoduct in Region A is extremely complex and only a preliminary account of its nature is given here. A short zone of transitional epithelium lies between the epithelium of the gonoduct and the germinal epithelium (Fig. 8, TE). The following observations, made on the epithelium of the gonoduct, are based both on wax models and on serial sections of Region A. The opening of the gonoduct into the lumen of the gonad is inconspicuous; it is formed by several slit-like openings which are surrounded by a group of concentric circular ridges of transitional epithelium. Within the gonoduct, a series of imbricating ridges of epithelium project into the lumen of the duct (Figs. 8 and 9). The lumen of the duct meanders among these ridges and in its circuitous course gives off blind sacs. There follows a series of ridges formed of epithelium that spiral along the axis of the gonoduct and that eventually fade away leaving the simple unobstructed lumen of Region B. The arrangement of the epithelial layer of the gonoduct in Region A, described above, is obvious in all mature specimens examined. It is not apparent at all in very young animals; in slightly older but still immature specimens it is represented by a region of thick epithelium that occludes the lumen of the gonoduct.

Region B: in contrast to Region A, this is the longest section of the gonoduct and also the simplest in terms of its relationships to the ray and of the complexity





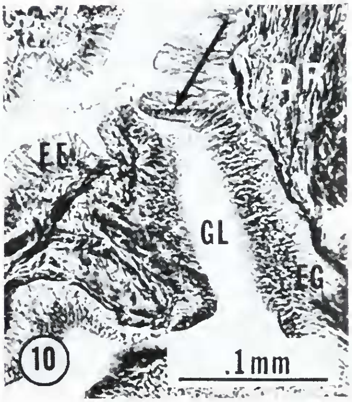


FIGURE 8. A longitudinal section of the gonoduct where it opens into the lumen of the gonad, showing the ridges of epithelium of Region A of the gonoduct, CR (PTAH). Notice the continuity between the germinal epithelium of the gonad and the epithelium of the gonoduct with transitional epithelium intervening. Symbols used are: GCS, genital coelomic (perihaemal) sinus; GE, germinal epithelium of the gonad; GHS, genital haemal strand; L, lumen of the gonad; PO, primary oocyte; TE, transitional epithelium of the gonoduct.

FIGURE 9. Photograph of a wax model reconstructed from serial sections of the gonoduct in Region A (female). Notice the primary oocyte which has a diameter of about 150 μ. Symbols used are: CR, cross-ridges of epithelium in Region A of the gonoduct; GHS, genital haemal strand; M, mouth of the gonoduct; PO, primary oocyte; TE, transitional epithelium.

FIGURE 10. Longitudinal section of the terminal portion of the gonoduct in Region D, showing a subsidiary gonoduct opening at the surface of the ray (PTAH). Notice the distinct change in the epithelia just inside the mouth of the gonoduct (arrow); the opening to external environment is lined by the external epithelium and not by the epithelium of the gonoduct. Symbols used are: DR, dermis; EE, external epithelium; EG, epithelium of the gonoduct; GL, lumen of the gonoduct.

of its tissues (Figs. 1 and 6). Throughout this region, the gonoduct is enclosed by the subperitoneal connective tissue of the body wall. Here, as in Region A, the connective tissue fibers of the gonoduct run longitudinally parallel to the lumen, and the layer that they constitute is thrown into longitudinal folds. These folds are irregularly rounded, some being very short and others long and slender, rising into the epithelial layer (Fig. 6). In the epithelial layer, flagellated cells ride the crests and troughs of the underlying connective tissue, but their free ends all rise to a common level giving a fairly uniform surface to the lumen. To accomplish this, some of the cells are much taller than others; the bases of the tallest cells are very slender, often appearing as mere fibers.

Regions C and D: after proceeding for a variable distance along the coelomic pocket within the subperitoneal connective tissue layer, the gonoduct finally penetrates the wall of the ray. Upon doing so its connective tissue is bound in a new relationship with the dermis. All tissue layers of the gonoduct are similar in Regions C and D and with few exceptions are identical to those seen in Region B. In Region C, the gonoduct often appears roughly circular in cross-section, but usually flattens into a narrow tube near Region D where it is divided into subsidiary gonoducts. The subsidiary ducts have variable diameters, and it is usually impossible to determine which represents the primary gonoduct. There may be one or two main ducts, or all may be large, or all diminutive. Characteristically, the diameter of the lumen decreases as the ducts approach the surface of the ray. Gonoducts of very small diameter may appear to lack a distinct connective tissue layer, and these have an epithelium composed of a single layer of columnar cells. The gonopores are difficult to detect because the external epithelium is pursed over their openings.

Discussion

In spite of their small size, the gonoducts of *Asterias vulgaris* are structurally complex; some striking similarities and significant differences in morphology and histology can be brought out by comparing the gonoduct in *Asterias vulgaris* with those in other sea-stars that have been described by previous investigators.

As mentioned earlier, each gonoduct of a sexually mature specimen of either sex of *Asterias vulgaris* extends from the gonad to the body wall as a single tube and then becomes subdivided to form subsidary ducts that open separately in the external epithelium. This arrangement of the gonoduct was noticed in *Asterias rubens* by Müller and Troschel (1842) and is presumably found in other members of the Asteriidae; it may be characteristic of sea-stars in other families as well, although such information is not available. In other asteroids, the gonoducts are arranged quite differently. In *Solaster endeca,* for example, many ducts are present, and each arises from a separate tubule of the tuft-like gonad of this organism. These ducts pass to the body wall where they may fuse to form only one or a few main ducts that open in the external epithelium (Gemmill, 1911, 1912). In *Crossaster papposus*, separate gonoducts extend from each tubule of the tuft-like gonad to the body wall, but these do not fuse and consequently many gonoducts pass through the body wall and open in the external epithelium (Gemmill, 1911). It is unfortunate that so little information is available concerning the arrangement of the gonoduct in other sea-stars; such information might be useful in correlating the form of the gonoduct with its function in sea-stars with different methods of reproduction.

The association of the gonoduct with a coelomic pocket found in the wall of the ray occurs in many sea-stars. In *Asterias vulgaris* (Forcipulata, Asteriidae), as mentioned, the coelomic pocket is one of hundreds of similar structures opening into the coelom and extending through the body wall to form dermal branchiae. The gonoduct profits from its relationship with the subperitoneal connective tissue layer of the pocket by being conducted nearer the surface of the ray to the point where it opens in the external epithelium. Ludwig (1877) provides an illustration of such a relationship in *Echinaster fallax* (Spinulosa, Echinasteridae), although he does not mention it in his text. Cuénot (1887) noticed this relationship in several species of asteroids and believed that it was of considerable significance. He illustrates this association as it appears in *Marthasterias glacialis* (Forcipulata, Asteriidae) and mentions its occurrence in *Crossaster papposus* (Spinulosa, Solasteridae) and *Asterias rubens* (Forcipulata, Asteriidae). Richters (1912), in his study of *Linckia multiforis* (Phanerozonia, Linckiidae), gives an excellent figure accompanied by a text description indicating that in the serial gonads of this species, the gonoduct extending from each gonadal tuft is associated with a coelomic pocket. It is thus apparent that the relationship between the gonoduct and a coelomic pocket is similar in many distantly-related species of asteroids; in many sea-stars, however, such a relationship has not been reported.

In developmental terms, there is sound rationale for close association of the gonoduct with a coelomic pocket in the wall of the ray. In *Asterias vulgaris*, by the time the gonoduct begins to form, the dermis is already quite thick and tough. Presumably, it is much easier for the growing gonoduct to burrow along the wall of the ray in the subperitoneal connective tissue following this layer into a coelomic pocket, than to penetrate directly through the entire dermis of the ray. Near the dermal branchiae the connective tissue layer becomes thin, and only there does the gonoduct enter the dermis. Because of the widespread occurrence of this association between the gonoduct and a coelomic pocket in asteroids, it is likely that the gonoduct may develop similarly in sea-stars where it is arranged as it is in *Asterias*. Obviously, where such a relationship is absent the developing gonoduct must reach the surface of the ray in some other way.

A relationship between the gonoduct and a coelomic pocket in the wall of the ray is certainly not without functional significance in the adult sea-star. In *Asterias vulgaris* the folded elastic-like connective tissue and the crowded columnar epithelium of the gonoduct are capable of extreme expansion. Rapid release of gametes is facilitated by this expansion and would be impossible if the gonoduct passed through the entire body wall bound tightly in connective tissue on all sides. Considerable space is provided for such expansion since the gonoduct with its encasing subperitoneal connective tissue is anchored firmly to the dermis on one side only and extends freely into the coelomic pocket elsewhere.

The epithelial ridges found near the orifice of the gonoduct within the gonad (Region A) are another feature of the structure of the gonoduct of *Asterias vulgaris* that was recognizable in both sexes of all mature specimens observed. These ridges have never been mentioned in the literature on asteroids; in fact, Gemmill (1914) makes a point of stating that no barriers are present which would prevent spawning in females of *Asterias rubens*. Only Richters (1912) indicates such ridges in a figure of a sectioned gonad and gonoduct of *Linckia multiforis*, but he does not discuss them in his text. The purpose of these structures is problematical, although it is conceivable that they function to hold gametes in the gonad during the expansion that accompanies gametogenesis. The pressure exerted by the increase in size and numbers of gametes during gametogenesis is great, and the plugging mechanism provided by such ridges could be important in preventing leakage of mature or maturing gametes.

Further detailed studies on the structure of the gonoducts of other species of asteroids would provide information necessary in comparing the form and function of this important part of the reproductive system in several sea-stars with different methods of reproduction and would give the basis for a better understanding of the way in which gametes are released from gonad.

I thank Dr. John M. Anderson for his advice and guidance through the course of this study and for his careful review of the manuscript. I also thank Dr. W. Sack of Cornell University School of Veterinary Science for the use of his wax modeling equipment. Considerable assistance, advice, and encouragement were also provided by my wife, Wilise.

Summary

In *Asterias vulgaris* there are 10 separate units of the reproductive system, each with its own distinct gonoduct. The gonoduct forms late in the life of the sea-star as an outgrowth of the inner sac of the gonad. During its formation, each gonoduct grows from the gonad to the body wall where it burrows through a layer of connective tissue located below the parietal peritoneum. The gonoduct follows this subperitoneal connective tissue into a coelomic pocket (which ends externally in several dermal branchiae) and ultimately penetrates the dermis, where it divides into subsidiary ducts which open separately in the external epithelium of the interradius. The gonoduct consists of an outer elastic connective tissue layer continuous with both walls of the haemal sinus of the inner sac of the gonad and an inner epithelial layer continuous with the germinal epithelium of the gonad. Near the point where the gonoduct opens into the lumen of the gonad, the epithelial layer of the gonoduct forms cross-ridges which span the lumen of the duct and imbricate, partially blocking the lumen.

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